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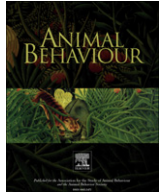
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Effect of weapon-supportive traits on fighting success in armed insects

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Male fighting frequently results in the evolution of traits used as weapons. These are often coupled with correlated modifications in other somatic traits (hereafter referred to as supportive traits), which are thought to support the weapon functionally. No previous studies have investigated whether supportive traits themselves affect fighting success. We evaluated this possibility in two armed insects, the beetle *Gnatocerus cornutus* and the bug *Riptortus pedestris*. Using a principal components analysis, we identified a subset of supportive traits that were associated with weapons in both species. The patterns of supportive structures differed between the two species, probably reflecting differences in the use of weapons during fights. In both species, fighting success was higher in males with enhanced supportive traits. It appears that weapon-supportive structures develop as the result of selection that favours coordination among multiple traits associated with fighting behaviour. Thus, our results provide rare evidence of the benefit of a supportive trait that is a clear example of phenotypic integration.

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Sexual selection can result in the exaggeration of morphological traits, such as the ornaments used for attracting mates (e.g. elongated tails of birds and the eyestalks of stalk-eyed flies) and weapons associated with male–male competition (e.g. the horns and mandibles of beetles; Darwin 1871; Andersson 1994; Shuster & Wade 2003; Emlen 2008). Enlargements in nontarget traits may accompany those in the primary targets of exaggeration (as reviewed in Husak & Swallow 2011), leading to coupling of exaggerated traits and correlated modifications in other somatic characters (Pigliucci & Preston 2004).

A well-known example is secondary sexual trait compensation. The production and maintenance of an exaggerated trait can be costly, in terms of predation and/or parasitism risk and energetic and physiological expenditure (Kotiaho 2001; Cotton et al. 2004; Okada et al. 2011a). These potential costs can be offset by the changes in somatic traits that compensate for the cost of exaggeration (Tomkins et al. 2005). Compensation has been suggested from morphological data in several species (Hedenstrom & Møller 1992; Andersson & Andersson 1994; Balmford et al. 1994; Tomkins et al. 2005; Husak et al. 2011). For example, in male barn swallows,

Hirundo rustica, and stalk-eyed flies, male wings are enlarged in addition to primary (exaggerated) ornaments, probably to offset the cost of carrying them (e.g. tail streamers and eyestalks, respectively; Møller et al. 1995; Husak et al. 2011).

Similar findings in nontarget traits have also been reported in several armed insects (Tomkins et al. 2005; Okada & Miyatake 2009): males with larger weapons have been found to possess larger traits (hereafter referred to as 'supportive traits') that help males to use their enlarged weapons. For example, a larger head, prothorax and forelegs (Okada & Miyatake 2004; Tatsuta et al. 2004; Tomkins et al. 2005; Okada et al. 2007) may act as supportive traits for male beetles that use their horns and mandibles to fight with rival males over access to females (Eberhard 1979; Otte & Stayman 1979; Emlen & Nijhout 2000). Supportive traits are also thought to be important structures in male combat (Otte & Stayman 1979), independent of the primary exaggerated traits. As such, they are predicted to increase male fighting success (Tomkins et al. 2005; Okada & Miyatake 2009). Weapon-supportive traits can also be compensatory traits during nonantagonistic situations, such as carrying large weapons during walking and thus compensation and support are not always mutually exclusive (see Tomkins et al. 2005). Nevertheless, in this study, we refer to these traits as supportive because we focus on the weapon-supportive function of nontarget traits during fighting, rather than cost compensation. The supportive traits should be selected concurrently with exaggerated weapon traits, and selection should favour a mechanism that provides suitable combinations of

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multiple traits in relation to fighting behaviour (Pigliucci & Preston 2004; Irschick et al. 2007, 2008).

Surprisingly, no studies to date have empirically tested the possibility that supportive traits influence fighting success. Therefore, we developed the current study to test this assumption in two species, the broad-horned flour beetle, *Gnatocerus cornutus*, and the bean bug, *Riptortus pedestris*. In both species, males use enlarged weapons (mandibles and modified hindlegs, respectively) to fight for mates, with fighting success positively influenced by weapon size. Since these structures are limited to males, and body sizes and these weapons have positive allometric relationships, they are good examples of exaggerated morphologies (*G. cornutus*: Okada et al. 2006; *R. pedestris*: Okada et al. 2011b). While male beetles use their mandibles to push, bite and lift up their opponents during combat, bean bugs use their hindlegs to kick, grasp and squeeze rival males (Yamane et al. 2010; Okada et al. 2011b). We used these two species with different types of weapon structures, head and hindlimbs, to explore how different body modules are modified by the exaggerations in different appendages.

To identify potential supportive traits, we used principal components analyses (PCA) and generalized linear models (GLMs) to find phenotypic correlations between weapons and somatic traits (see also Tomkins et al. 2005). Informative principal components (PCs) from the PCA were then used to assess whether fighting success is improved by possession of enlarged supportive characters.

METHODS

Gnatocerus cornutus

Culturing and morphological measurements

The *G. cornutus* beetle population originated from adults collected in Miyazaki City, Japan (31° 54', 131° 25'), and has been maintained in the laboratory of the National Food Research Institute, Japan, for approximately 50 years on a diet of wholemeal flour enriched with yeast. The beetle population has never been supplemented with wild-caught adults. We performed all rearing and experiments in a chamber maintained at 25 °C, 60% relative humidity, and with a photoperiod cycle of 16:8 h light:dark. All emerging adults were housed in separate wells of 24-well tissue culture plates (Cellstar; Greiner Bio-One, Frickenhausen, Germany) until the following experiment (see Okada & Miyatake 2010a for further details).

We randomly selected 100 males from the stock and measured nine body parts: mandible length, head width, prothorax length, prothorax width, elytra length, elytra width, forefemur length, midfemur length and hindfemur length. A dissecting microscope monitoring system was used to measure the length of each character as a straight-line distance between two points, to within 0.01 mm (Fig. 1). Each specimen was carefully positioned so its longitudinal and dorsoventral axes were perpendicular to the visual axes of the oculus. Of 100 males measured, we used 40 for the following experiments on fighting success.

Fighting success

To investigate which morphological components were associated with success in male fighting, we staged 20 contests between males using methods previously described elsewhere (Okada & Miyatake 2010a). Briefly, contests occurred 15–20 days after emergence and took place in an arena consisting of a plastic container (diameter: 17 mm; height: 20 mm) lined with filter paper (diameter: 17 mm). In each contest, two males were simultaneously introduced into the arena and their behaviour was observed for 30 min. This beetle lives under bark, where males probably establish territories for reproduction (Yoshida 1958). They guard their territories and usually evict other nearby males (Okada

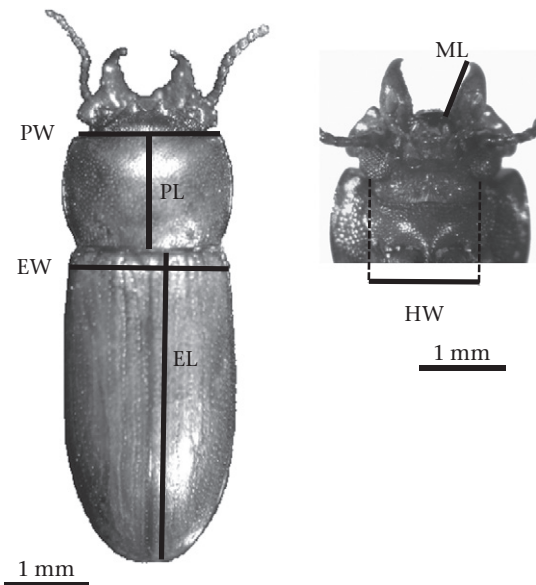


Figure 1. Somatic characters of *G. cornutus* that were measured as potential supportive traits. ML: mandible length; HW: head width; PL: prothorax length; PW: prothorax width; EL: elytra length; EW: elytra width.

et al. 2010; Okada & Miyatake 2010a). Thus, it is possible to make two males fight by putting them in a small arena. The winner of the contest was the male that pushed his opponent and tried to chase him out of the arena. Winners and losers can be clearly defined, because losers run away from the opponent and never resume agonistic behaviour (Okada & Miyatake 2010a). The difference in mandible length between all pairs of contestants was <0.01 mm, which was the minimum in our measurement system. This difference between contestants was less than 2.6% of mandible size range (Table 1), which allowed us to control for an effect of mandible size on fighting success (Okada & Miyatake 2010a). Size differences in other traits were 14–25% of trait size ranges (Table 1).

Riptortus pedestris

Culturing and morphological measurements

The stock population of *R. pedestris* originated from adults collected in 2009 from soya bean, *Glycine max*, fields in Okayama City, Japan (31°41' N, 131°54' E). Males compete for territories on the leaves and stems of their host plant, where they mate and reproduce (Natuhara 1985). Bugs were reared on an excess of medium containing seeds of soya bean and red clover, *Trifolium pratense*, and water containing ascorbic acid (0.05%). They were housed in a chamber measuring 2400 × 2400 mm and 2400 mm high (CC-T2000, Sanyo, Osaka, Japan) kept at 25 °C and 60% relative humidity. Nymphs were maintained in plastic cups (diameter: 100 mm; height: 40 mm) at densities of 10–20 individuals. Each emerging adult was housed in a separate petri dish until the fighting experiment (see below). Further details on housing are discussed in Okada et al. (2011b).

We randomly selected 120 males from the stock to measure eight body parts: head width, thorax width, thorax length, abdomen width, abdomen length, forefemur length, midfemur length and hindfemur length (Fig. 2), employing the same system used for the beetles. Because we matched the size of paired males (see below), we used only 30 of 120 males measured for the following experiment.

Fighting success

We staged 15 contests between males 15–20 days after emergence, using methods previously described elsewhere (Okada et al.

Table 1Size, range and between-contestant difference of the morphological traits of *G. cornutus* and *R. pedestris*

Trait	Population mean \pm SE	Size range (minimum – maximum)	Size difference between contestants (mean \pm SE, (% of size range))
<i>G. cornutus</i>			
Mandible length (mm)	0.3981 \pm 0.0048	0.39 (0.18–0.57)	<0.01 (<2.56)
Prothorax width (mm)	1.2135 \pm 0.0034	0.13 (1.16–1.29)	0.0220 \pm 0.0041 (16.92)
Prothorax length (mm)	0.9800 \pm 0.0025	0.14 (0.92–1.06)	0.0230 \pm 0.0041 (16.43)
Elytra width (mm)	1.2721 \pm 0.0028	0.14 (1.21–1.35)	0.0340 \pm 0.0041 (24.29)
Elytra length (mm)	2.4769 \pm 0.0049	0.21 (2.38–2.59)	0.0455 \pm 0.0067 (21.67)
Head width (mm)	0.7863 \pm 0.0042	0.27 (0.63–0.90)	0.0380 \pm 0.0075 (14.07)
Forefemur length (mm)	0.6676 \pm 0.0038	0.16 (0.59–0.75)	0.0285 \pm 0.0036 (17.81)
Midfemur length (mm)	0.6441 \pm 0.0040	0.16 (0.58–0.74)	0.0370 \pm 0.0055 (23.13)
Hindfemur length (mm)	0.7604 \pm 0.0044	0.23 (0.64–0.87)	0.0415 \pm 0.0061 (18.04)
<i>R. pedestris</i>			
Hindfemur length (mm)	7.6656 \pm 0.0478	2.52 (6.38–8.80)	0.0080 \pm 0.0044 (0.32)
Thorax width (mm)	3.0863 \pm 0.0174	1.14 (2.40–3.54)	0.2280 \pm 0.0606 (20.00)
Thorax length (mm)	5.3442 \pm 0.0162	0.72 (4.97–5.69)	0.1740 \pm 0.0478 (24.17)
Abdomen width (mm)	3.7183 \pm 0.0156	0.84 (3.29–4.13)	0.2300 \pm 0.0458 (27.38)
Abdomen length (mm)	6.8369 \pm 0.0205	0.98 (6.28–7.26)	0.1190 \pm 0.0228 (12.14)
Head width (mm)	2.6133 \pm 0.0074	0.38 (2.42–2.80)	0.0430 \pm 0.0068 (11.32)
Forefemur length (mm)	4.0678 \pm 0.0161	0.75 (3.73–4.48)	0.1530 \pm 0.0420 (20.40)
Midfemur length (mm)	4.2178 \pm 0.0151	0.76 (3.89–4.65)	0.2200 \pm 0.0464 (28.95)

Population mean and size range were calculated from males used for morphological measurement in each trait. In *G. cornutus*, size difference of mandible length between contestants was controlled to the minimum of our measurement system (<0.01 mm); thus mean and SE were not calculated.

2011b). Briefly, the arena consisted of a plastic container (diameter: 90 mm; height: 15 mm) lined with filter paper (90 mm diameter). Introduction of two males into a small arena can induce male combat because of the males' territorial habits. For each contest, two males were simultaneously introduced into the arena and their behaviour was observed for 30 min. The winner was the male that pushed his opponent and tried to chase him out of the arena. The loser was the one that retreated from the opponent and never resumed a fight against the winner (Okada et al. 2011b).

To control for an effect of hindfemur size on fighting success, we ensured that the difference in hindfemur length between contestants was <0.04 mm. The difference between contestants was less than 1.6% of the range of hindfemur length (Table 1). Size differences in other traits were 10–30% of trait size ranges (Table 1).

Statistical Analysis

Since all the traits were highly correlated and multiple regression was unsuitable because of the high multicollinearity, we used a PCA to partition the variance attributable to the various traits using a correlation matrix (Tomkins et al. 2005). This allowed us to examine developmental integration of the phenotypic traits measured for each species. In general, PCs can explain overall variation until the cumulative proportion of variation becomes 80–90% (Jolliffe 2002). In this study, PCs were regarded as informative until their cumulative contribution exceeded 85%.

To determine which traits interacted with the males' primary weapons, we constructed a GLM for each species, using normal error distributions and an identity link. Weapon size (mandible length in *G. cornutus* and hindfemur length in *R. pedestris*) was entered as the dependent variable and informative PCs were included as predictor variables. Because the relationship between weapon and body sizes departs from linearity in both species (Okada & Miyatake 2010b; Okada et al. 2011b) and shows 'positive allometry' (sensu Gould 1966), actual weapon size was log transformed prior to inclusion in the GLM (Tomkins et al. 2005; Okada & Miyatake 2010b). We used a reduced model that removed nonsignificant interaction terms from the full model (Grafen & Hails 2002).

To investigate which PCs were associated with fighting success (a binomial variable, for which 1 = won and 0 = lost), we constructed a GLM with binomial errors and a logit link (Hardy & Field 1998; Pomfret & Knell 2006). Fighting success was entered as the dependent variable, and informative PCs and weapon size (mandible length in *G. cornutus* and hindfemur length in *R. pedestris*) were included as predictor variables. Additionally, to investigate whether each trait was associated with fighting success, we constructed a GLM with fighting success as the dependent variable and each nontarget trait as the predictor variable. We adopted a reduced model that removed nonsignificant interaction terms from the full model (Grafen & Hails 2002).

RESULTS

Gnatocerus cornutus

The PCA generated eight PCs, four of which were informative (Table 2). The percentages of morphological variations explained

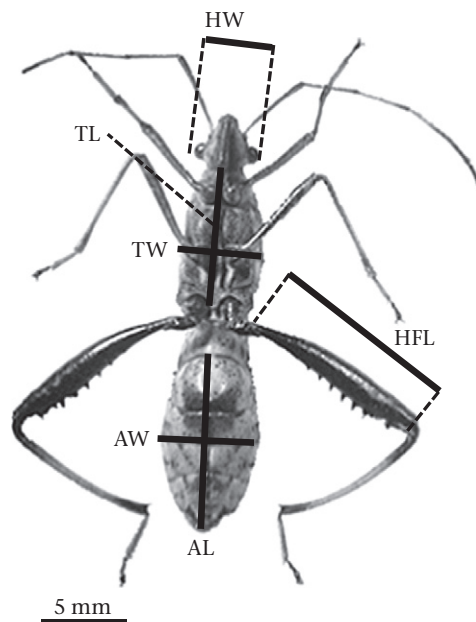


Figure 2. Somatic characters of *R. pedestris* that were measured as potential supportive traits. HW: head width; TL: thorax length; TW: thorax width; AL: abdomen length; AW: abdomen width; HFL: hindfemur length.

Table 2Factor loadings from the principal components analyses of morphological traits in *G. cornutus* and *R. pedestris*

Trait	PC1	PC2	PC3	PC4
<i>G. cornutus</i>				
Percentage	64.63	9.68	7.84	5.53
Prothorax width	0.9469	−0.0861	0.0169	−0.0983
Prothorax length	0.8025	0.3601	0.1424	−0.1134
Elytra width	0.7039	−0.2300	0.5691	0.3055
Elytra length	0.8412	− 0.3684	−0.1138	0.0260
Head width	0.6993	0.4849	−0.2993	0.3363
Forefemur length	0.8174	0.3360	0.2004	−0.1830
Midfemur length	0.8101	−0.1758	−0.1485	− 0.3698
Hindfemur length	0.7833	−0.2642	− 0.3439	0.2057
<i>R. pedestris</i>				
Percentage	42.58	26.14	11.39	7.28
Thorax width	0.8224	− 0.4566	−0.0983	0.0763
Thorax length	0.7066	0.4431	−0.2813	0.0663
Abdomen width	0.5306	− 0.7015	−0.2471	0.2806
Abdomen length	0.7456	0.4489	−0.0705	0.1312
Head width	0.7851	0.0375	0.0015	− 0.5863
Forefemur length	0.5316	−0.2661	0.7811	0.0822
Midfemur length	0.2609	0.8120	0.1796	0.2307

The highest loading variables for each PC are indicated in bold.

by PC1–4 were 64.63%, 9.68%, 7.84% and 5.53%, respectively, indicating that contributions of PC2–4 were smaller than that of PC1. PC1 loaded positively for overall size. Prothorax width had the highest loading weight, which suggests that it is suitable as a body size index, as found previously (Okada & Miyatake 2009, 2010a). PC2 loaded positively for prothorax length, head width and forefemur length, but negatively for elytra length. Thus, higher PC2 represents body shape with larger anterior body parts and smaller posterior body parts. PC3 loaded positively for elytra width and negatively for hindfemur length, while PC4 loaded negatively for midfemur length.

We found a significant positive relationship between mandible length and both PC1 (body size) and PC2 (body shape and forefemur length); however, mandible length was not associated with PC3 (elytra width/hindfemur length) or PC4 (midfemur length; Table 3). PC1 was included in the final, reduced model so that the remaining PC2 effects were on relative mandible length. Therefore, the relative mandible length is positively associated with prothorax length, head width and forefemur length, but negatively with elytra length. This means that males with relatively large mandibles have relatively large head, prothorax and forefemur.

Table 3Results of generalized linear models exploring the relationships between weapon size and other somatic characters in *G. cornutus* and *R. pedestris*

Predictor variables	df	Coefficient±SE	Mean square	F	P
<i>G. cornutus</i>					
PC1 (body size)	1	0.0380±0.0040	0.7377	90.9326	<0.0001
PC2 (body shape and forefemur length)	1	0.0267±0.0103	0.0545	6.7151	0.011
PC3 (elytra width/hindfemur length)	1		0.0125	1.5378	0.218
PC4 (midfemur length)	1		0.000002	0.0002	0.989
Error	95		0.0081		
<i>R. pedestris</i>					
PC1 (body size)	1	0.0322±0.0020	0.3667	269.5337	<0.0001
PC2 (body shape and midfemur length)	1	0.0126±0.0025	0.0345	25.3661	<0.0001
PC3 (forefemur length)	1		0.00009	0.0631	0.802
PC4 (head width)	1		0.0017	1.2456	0.267
Error	115		0.1565	0.0014	

Nonsignificant interaction terms have been removed from the model.

We observed male aggressive behaviours in all contests. The GLM revealed a significant positive relationship between fighting success and PC2, but no relationships between aggressive performance and mandible length or PCs 1, 3 or 4 (Table 4). When each trait was used as a predictor variable in a GLM, we detected a significant negative relationship between fighting success and elytra length (coefficient ± SE = −13.2833 ± 6.9666; $\chi^2_1 = 4.037$, $P = 0.045$), but there were no relationships between fighting success and other traits (prothorax width: $\chi^2_1 = 0.206$, $P = 0.650$; prothorax length: $\chi^2_1 = 2.011$, $P = 0.156$; elytra width: $\chi^2_1 = 0.792$, $P = 0.373$; head width: $\chi^2_1 = 1.991$, $P = 0.158$; forefemur length: $\chi^2_1 = 0.127$, $P = 0.721$; midfemur length: $\chi^2_1 = 2.031$, $P = 0.154$; hindfemur length: $\chi^2_1 = 3.253$, $P = 0.071$).

Riptortus pedestris

The PCA generated seven PCs, four of which were informative (Table 2). As in the beetles, PC1 accounted for overall body size. PC2 loaded positively for thorax, abdomen and midfemur length, but negatively for thorax and abdomen width; thus, this variable describes body shape in that large PC2 indicates a slender body with longer midfemur. PC3 loaded positively for forefemur length, while PC4 loaded negatively for head width (Table 2).

The GLM revealed a significant positive relationship between hindfemur length and both PC1 (body size) and PC2 (body shape and midfemur length). However, hindfemur length was not significantly associated with PC3 (forefemur length) or PC4 (head width; Table 3). PC1 was included in the final model so that the remaining PC2 effects were on relative weapon size. Therefore, the relative hindfemur length is positively associated with thorax length, abdomen length and midfemur length, but negatively with thorax width and abdomen width.

Males did not fight in five of 15 observations for unknown reasons; thus our final analysis only included data from 10 aggressive encounters. Male fighting success was significantly positively related to PC2, but was not associated with hindfemur length or PCs 1, 3 or 4 (Table 4). When each trait alone was used as a predictor variable in a GLM, we detected a significant positive relationship between fighting success and midfemur length (coefficient ± SE = 9.9788 ± 4.5481; $\chi^2_1 = 8.718$, $P = 0.003$), and negative relationships between fighting success and thorax and abdomen widths (thorax width: −9.6860 ± 4.3283; $\chi^2_1 = 8.482$, $P = 0.004$; abdomen width: −14.9929 ± 6.9684; $\chi^2_1 = 11.581$, $P = 0.0007$). Other traits did not have significant effects on contest outcome (thorax length: $\chi^2_1 = 0.014$, $P = 0.906$; abdomen length:

Table 4Results of the generalized linear models exploring the effects of morphological characters on fighting success in *G. cornutus* and *R. pedestris*

Predictor variables	df	Coefficient±SE	χ^2	P
<i>G. cornutus</i>				
Weapon size (mandible length)	1		0.3434	0.558
PC1 (body size)	1		0.4986	0.480
PC2 (body shape and forefemur length)	1	2.9969±1.2477	23.6599	<0.0001
PC3 (elytra width/hindfemur length)	1		0.7056	0.401
PC4 (midfemur length)	1		0.0528	0.818
<i>R. pedestris</i>				
Weapon size (hindfemur length)			1.5715	0.210
PC1 (body size)	1		0.4887	0.485
PC2 (body shape and midfemur length)	1	2.8843±1.3364	13.1567	0.0003
PC3 (forefemur length)	1		1.4944	0.222
PC4 (head width)	1		0.1446	0.704

Nonsignificant interaction terms have been removed from the model.

$\chi^2_1 = 0.374$, $P = 0.541$; head width: $\chi^2_1 = 0.012$, $P = 0.912$; fore-femur length: $\chi^2_1 = 1.582$, $P = 0.209$).

DISCUSSION

In both *G. cornutus* and *R. pedestris*, PCA indicated that several body parts are positively associated with the animals' exaggerated weapon characters. This morphological feature indicates that these body parts act as weapon-supportive traits (Otte & Stayman 1979; Tomkins et al. 2005). Indeed, for both broad-horned flour beetles and bean bugs, fighting success was significantly increased by enhancement of these traits, suggesting that they act as supportive traits. Thus, we have provided the first empirical evidence, to our knowledge, that supportive traits are beneficial in providing structural support for sexually selected weaponry.

During territorial encounters, male *G. cornutus* push, bite and lift up opponents; a process involving not only their enlarged mandibles, but also their prothorax and forelegs (Okada & Miyatake 2009). Indeed, our results showed that relative mandible size was positively associated with forefemur, head and prothorax size, indicating that these latter three characters are supportive traits that enhance the benefit of possessing the primary weapon. Similar findings have been reported in other armed beetles (Otte & Stayman 1979; Tomkins et al. 2005). The negative association between mandible/supportive character sizes and elytra length/wing area are likely to be the result of resource competition between these characters (Okada & Miyatake 2009). Consistent with the factor loadings in PC2, elytra length had a negative effect on contest outcome, but we could not detect any effects of other traits. In size-matched contests, trait size differences between contestants are fairly small; therefore the effect of one trait could have been masked by the effects of other traits, and single effects were not fully evaluated. Unfortunately, we could not evaluate the sole effect of a single trait by equalizing the sizes of all other traits owing to the limitation in morphological variation. Given these results, we conclude that a certain combination of nontarget traits contributes to fighting ability, but independent effects of nontarget traits should be evaluated precisely in further studies.

During aggressive *R. pedestris* encounters, males turn their backs to their opponents and kick them with exaggerated hindlegs that are supported by strong midfemora (Okada et al. 2011b). Additionally, males often lift up their abdomens and perform displays towards their opponents (Okada et al. 2011b). Given these behaviours, we were not surprised to find positive associations between hindfemora size and thorax, abdomen and midfemur length; these three characters appear to be supportive traits for the exaggerated hindfemora. These results are similar to those of Tomkins et al. (2005), who detected positive relationships between earwig forceps and hindleg size. As predicted from PC2, midfemur length had a positive effect, and thorax width and abdomen width had negative effects on contest outcome, supporting the hypothesis that a large midfemur contributes to fighting success. In contrast, thorax length and abdomen length had no significant effects. As in *G. cornutus*, there is a certain combination of nontarget traits that provides a suitable body shape for combat (i.e. slender body with long midfemur), although independent effects of some nontarget traits require further investigation.

Cumulatively, our results indicate that most characters that are positively associated with weapons in *R. pedestris* and *G. cornutus* can be thought of as supportive traits. The interspecific differences in which body parts are associated with the weapon and how probably reflect differences in the ways in which weapons are used during aggressive encounters. The supportive structures may ultimately emerge through male fighting, since successful males (i.e. those with the better supportive traits) gain access to females,

and mate with them (Okada & Miyatake 2009). Over time, this leads to changes in body shape across the population, such that exaggerated weaponry is associated with appropriate supportive structures, generating an overall body shape that is more suitable for fighting (e.g. Otte & Stayman 1979; Emlen 2008).

Fighting success in these two focal species is positively impacted by both larger weapon size (Okada et al. 2006, 2011b) and enhanced supportive traits. Since fighting success is a major determinant of male fitness in general (reviewed in Andersson 1994; Shuster & Wade 2003), the weapon and its supportive traits are likely to be under correlational selection. As a result, they should be genetically correlated and develop in an integrated manner. In a previous study in *G. cornutus*, we found positive genetic correlations between the weapon and its supportive traits, suggesting that these characters have undergone correlational selection (Okada & Miyatake 2009). This association among the weapon and its supportive traits is a clear example of phenotypic integration, which refers to coordination among functionally related multiple traits (see details in Olson & Miller 1958; Pigliucci 2003; Pigliucci & Preston 2004; Klingenberg 2008). Phenotypic integration results from correlational selection on a particular trait and other somatic traits, where the variance in the relationship between traits is reduced by selection (Cheverud 1996; Wagner & Altenberg 1996; LeBas et al. 2003; Klingenberg 2004).

Conclusions

We empirically examined whether supportive traits for weapons improved performance in male–male contests. Our results indicate the presence of coordination among multiple, functionally related traits (Pigliucci & Preston 2004; Klingenberg 2008). Since supportive structures for exaggerated weapon traits, as well as secondary sexual trait compensation, are thought to be one of the best examples of phenotypic integration (Tomkins et al. 2005), further explorations of integration between exaggerated traits, supportive characters and fighting/display behaviours will increase our understanding of the evolution of complex, exaggerated morphologies.

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